EVOLUTION OF NIDIFICATION IN THE SCARABAEINAE (COLEOPTERA, SCARABAEIDAE)[1]

GONZALO HALFFTER
Instituto de Ecologia
Apartado Postal 18-845
México 18, D.F.

Quaestiones Entomologicae
13: 231-253 1977

This paper updates what is known about evolution of nidification in the Scarabaeinae. This process is one of the clearest examples of strategy K, accentuated by extreme reduction of the female genital apparatus (an ovary with a single ovariole), which in the more evolved groups produces very few eggs.

There are two evolutionary lines of nidification in the Scarabaeinae, and, on the basis of each one, there is a response to the ecological problems of exploiting excrement of large herbivores (rapid drying out, competition for the food mass and competition with flies). Nidification patterns in both lines are expressed as differences in food handling processes by adults.

In the first line, food for nidification is buried in a previously excavated gallery. The Group I pattern, which is the most primitive, includes a sequence of examples which range from simply packing a dung "sausage" (similar to the "sausages" that adults pack for their food in this entire line), to making a pear-shaped brood-ball, passing through intermediate stages of isolating the food destined for each larva from the food for other larvae of the same brood.

Group II and Group III patterns both derive from the Group I pattern. In the Group II pattern, the brood-ball is protected by a well laid-out layer of earth, which also protects the egg cell; the Group III pattern includes brooding behavior for the entire larval development period, in a nest housing several brood-balls. In both groups, intersexual collaboration develops on the basis of the first attempts that are found in group I.

The second evolutionary line has as its starting point the rolling (and in the majority of cases the previous making) of a ball of excrement, that is carried a certain distance and buried in a shallow excavation. Pattern IV is basic, which presents variations in method of rolling and collaboration between sexes. The Group V pattern is derived from this group, with formation of multiple nests cared for by the female and a well-marked bisexual collaboration in nidification.

Group VI adults do not roll, but prepare many balls for nidification. Nidification is complex and in some species includes a destruction by the father of the brood-balls, that until that moment have received special care in a multiple nest; finally, construction of a definitive multiple nest is achieved, very elaborately and with efficient care by the mother. In this group different degrees of bisexual cooperation are evident.

Groups I to IV were proposed previously; Groups V and VI are proposed in this paper. The most significant new data (published or not) of the last ten years are cited. Also indicated are the ecological pressures that determine similar behavior patterns in the two evolutionary lines (various cases of this type of convergence are cited). Also, some adaptations of the Australian Scarabaeinae linked to the lack of bovine-type excrement (before introducing cattle), and to the characteristics of marsupial pellets: small masses, rapidly hardened and desiccated, and scattered sparsely over extensive areas.

Este trabajo es una puesta al día de lo que se conoce sobre evolución de la nidificación en la subfamilia Scarabaeinae. Este proceso es uno de los ejemplos más claros de estrategia K, acentuada por la extrema reducción del aparato genital (un ovario con un sólo ovariolo) que en los grupos más evolucionados produce muy pocos huevos.

En la nidificación del grupo se presentan dos lineas evolutivas, en la base de cada una de las cuales se encuentra una respuesta a la problemática ecológica del excremento de los grandes herbivoros (rápida desecación, intensa agregación y compet-

---

[1] Invitational paper, submitted for publication at my request. – Editor.

encia en la masa de alimento, competencia con moscas). En ambas líneas, las pautas de nidificación son un derivado de los procesos de manejo del alimento por el adulto.

En la primera línea, el alimento para la nidificación es enterrado en una galería previamente excavada. El grupo I, el más primitivo, presenta una secuencia de ejemplos que incluyen desde el simple empaque de una "salchicha" de excremento (semejante a las "salchichas" que en toda esta linea empacan los adultos para su alimentación), hasta la elaboración de una bolanido piriforme, pasando por etapas intermedias de aislamiento creciente del alimento destinado a cada larva.

Del grupo I derivan el grupo II, en el que la bolanido queda protegida por una capa bien dispuesta de tierra, existiendo también una protección de la celda del huevo; y el grupo III con cuidados de la madre durante todo el tiempo del desarrollo larval, en un nido múltiple formado por varias bolas-nido. En ambos grupos la colaboración entre los sexos se desarrolla a partir de los primeros ensayos que se encuentran en el grupo I.

La segunda linea evolutiva tiene como punto de partida el rodaje (y en la mayor parte de los casos elaboración previa) de una bola de excremento, que es llevada a una cierta distancia y enterrada a poca profundidad. El grupo básico dentro de esta linea es el IV, que presenta variantes en la forma del rodaje y en la colaboración entre los sexos. De este grupo, deriva el V, con formación de nidos múltiples cuidados por la hembra y una colaboración bisexual bien marcada en la nidificación.

El grupo VI, no rueda, pero si prepara muchas bolas para la nidificación. Esta es compleja e incluye en algunas expecies una destrucción por los padres de las bolas - nido que hasta ese momento han recibido cuidados esmerados en un nido múltiple; finalmente se llega a la construcción de un nido múltiple definitivo, muy elaborado y con eficientes cuidados de la madre. En este grupo se presentan diversos grados de cooperación bisexual.

Los grupos I a IV fueron propuestos por Halffter y Matthews (1966), los grupos V y VI se proponen en este trabajo. En todos los casos se citan los nuevos datos más significativos de los últimos diez años (publicados o no); asi como las presiones ecológicas que determinan respuestas similares en las dos líneas evolutivas (se citan varios casos de este tipo de convergencia). También, algunas adaptaciones de los Scarabaeinae australianos ligados a la falta de excremento tipo vacuno (antes de la introducción del ganado) y a características de los pellets de los marsupiales: pequeñas masas, rápidamente endurecidas y desecadas, dispersas en grandes extensiones.

INTRODUCTION

Halffter and Matthews (1966) published the first overall analysis of natural history of dung beetles comprising the subfamily Scarabaeinae in which they interrelated nidification (nest building), feeding behavior, ecological distribution and classification. The purpose of this study is to update their discussion by analyzing the most important discoveries (published or not) that have taken place in the last ten years and to present an overall hypothesis on evolution of nidification behavior in the subfamily.

Within the Coleoptera nidification and intersexual relations in Scarabaeinae are among the best suited for an evolutionary analysis because of the variety and high level of complexity attained, the most advanced being incipient subsocial behavior. There are also structural modifications concomitant with evolution of nidification. Most striking is reduction of the female reproductive system to a single ovariole - a characteristic of the subfamily (Fig. 1). This reduction goes hand in hand with an extraordinarily low fecundity (Halffter and López 1977).

A salient feature of natural history of scarabaeids, especially of larvae, but adults, too, is connection with the soil. Relationship to soil is most profound, in the three sapro-coprophagous subfamilies Aphodiinae, Geotrupinae and Scarabaeinae. In Scarabaeinae, development of coprophagy and concomitant adult behavior patterns are determined by ecological characteristics of the excrement-soil system. Excrement is exposed on the surface to rapid desiccation and to flies, two factors which impede its use by beetles. Therefore, among dung beetles various behavior patterns have emerged which protect usable quantities of excrement destined for use as food.

Behavior patterns developed for feeding were, in turn, the basis for evolution of different approaches to nidification. The obvious starting point for establishment of evolutionary trends and nidification groups is food handling behavior, essentially handling of excrement of large herbivores. Scarabaeinae have a two-fold approach to this problem: 1) dung is packed into a burrow made beforehand; 2) a ball of dung is made on the surface, rolled, and then buried at a certain distance from the source.

Each solution corresponds to well-defined behavior patterns which are accompanied by

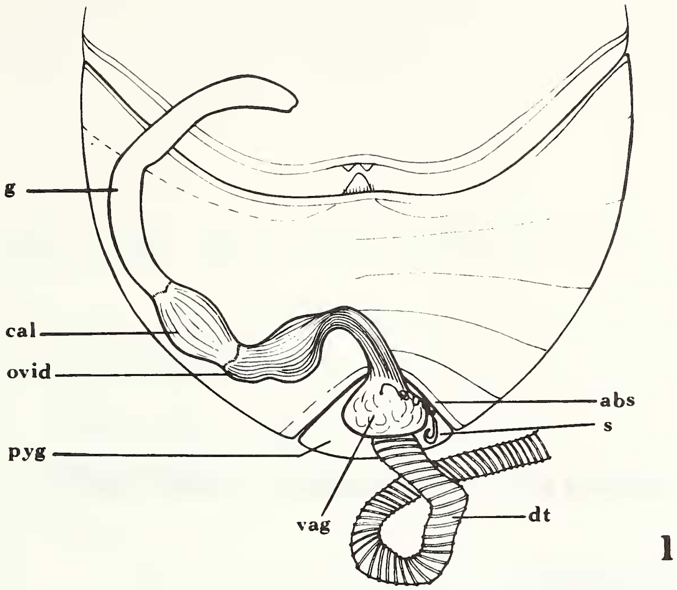


Fig. 1. *Phanaeus daphnis* Harold. Reproductive tract of a recently emerged female; note there is no distinction between germarium and vitellarium. abs - last abdominal sternum; cal - calyx; dt - digestive tract; g - germarium; ovid - oviduct; pyg - pygidium; s - spermatheca; vag - vagina (Halffter and Lõpez 1977).

striking morphological characteristics: stout, strong legs of burrowers which are well suited for digging; elongated and curved hind legs of ball-rolling adults.

The first solution (Fig. 2 & 3), *in situ* burying, is characteristic of four scarabaeine tribes (Onthophagini, Oniticellini, Onitini and Coprini) as well as of the subfamily Geotrupinae which is more primitive in its feeding and reproduction behavior than Scarabaeinae. The second solution is typical of the Scarabaeini and, with important modifications, of the Eurysternini, both tribes of Scarabaeinae.

For the first solution, the least evolved forms (designated Group I) are those in which the nest is very similar to feeding burrows. From this group emerge two evolutionary trends: the Group II trend, in which a female protects the brood-ball with an outer layer of soil but does not care for it once finished; and the Group III trend, in which a multiple nest (with several brood-balls) is tended by a female until emergence of her offspring.

For the second solution (Fig. 4 and 5), that is formation and rolling of a ball, which is typical of Group IV, there are several recognizable variations based upon protection or non-protection of the brood-ball with an outer layer of clay. Furthermore, in some Australian Canthonina, considered primitive by Matthews (1974), ball formation on the surface from a large dung mass has not developed, even though pellet rolling occurs. Group V, a derivative of Group IV, is similar to Group III in formation of multiple nests that are made and tended by female and male. Group VI, known in some Eurysternini, has uncertain behavioral affinities with other groups. Groups I-IV were proposed by Halffter and Matthews (1966); I here propose V and VI as a result of studies since then.

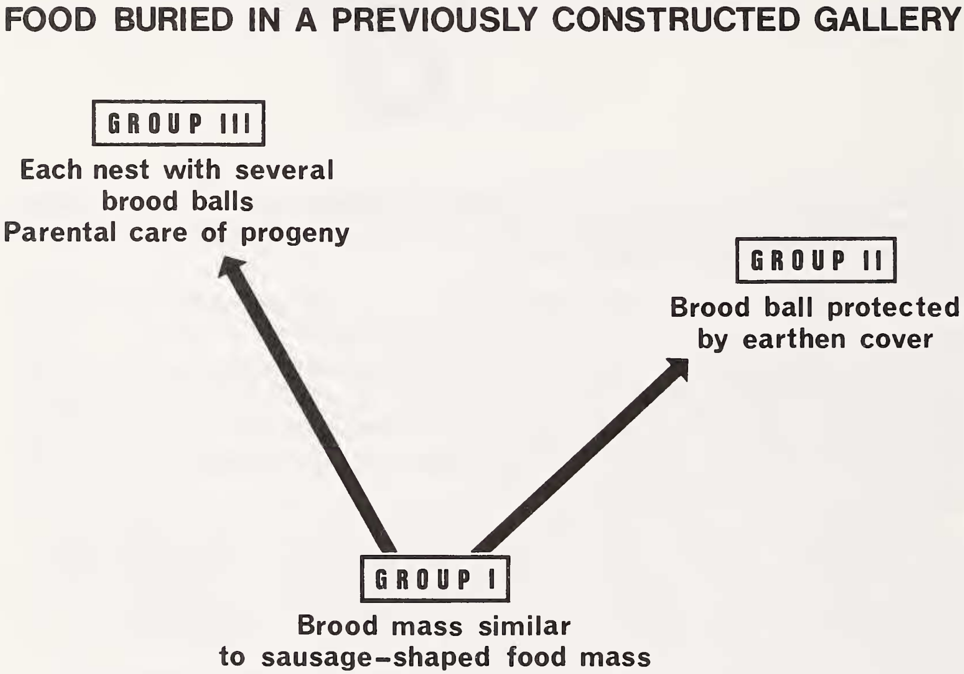

FOOD BURIED IN A PREVIOUSLY CONSTRUCTED GALLERY
GROUP III
Each nest with several brood balls
Parental care of progeny
GROUP II
Brood ball protected by earthen cover
GROUP I
Brood mass similar to sausage-shaped food mass

Fig. 2.

TAXONOMIC COMPOSITION

GROUP I: ONTHOPHAGINI
ONITICELLINI (in part)
ONITINI
COPRINI:
Dichotomiina (great majority)

GROUP II: COPRINI:
Phanaeina
Dichotomiina (*D. torulosus*)

GROUP III: COPRINI:
Coprina
SCARABAEINI:
Canthonina (*Cephalodesmius* only)

Fig. 3.

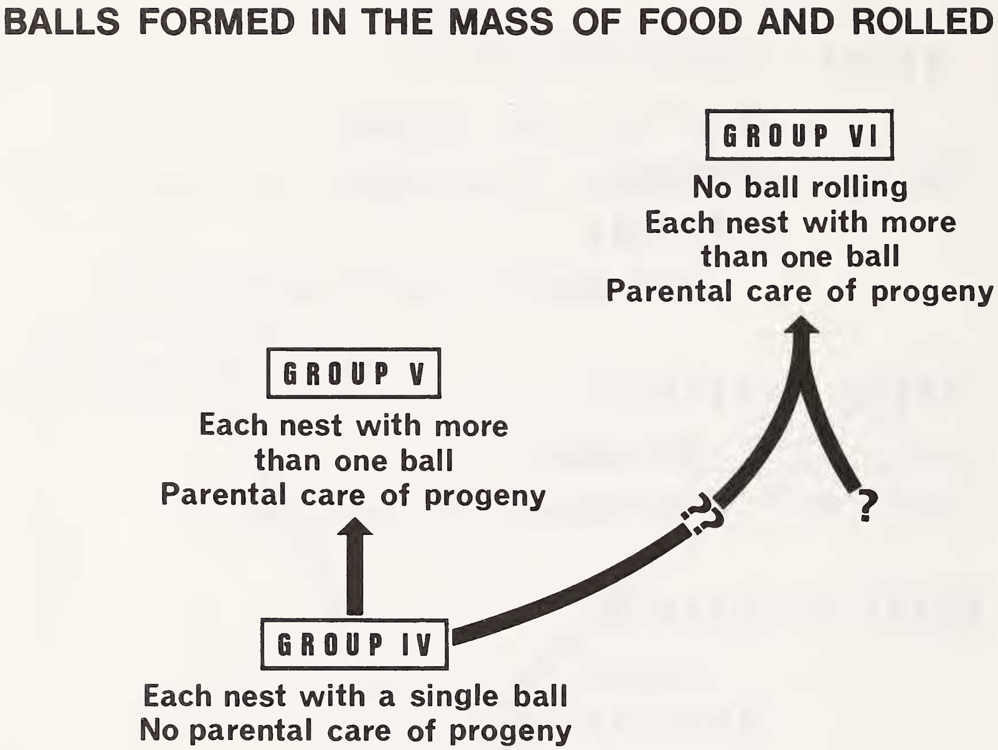

BALLS FORMED IN THE MASS OF FOOD AND ROLLED
GROUP VI
No ball rolling
Each nest with more than one ball
Parental care of progeny
GROUP V
Each nest with more than one ball
Parental care of progeny
??
?
GROUP IV
Each nest with a single ball
No parental care of progeny

Fig. 4.

TAXONOMIC COMPOSITION

GROUP IV: SCARABAEINI (except some Canthonina)

GROUP V: SCARABAEINI (some Canthonina)

GROUP VI: EURYSTERNINI

incertae sedis Oniticellus cinctus

-ONITICELLINI

Fig. 5.

DETAILS OF BEHAVIOR PATTERNS

Group I

Nidification behavior of this group is characterized by oviposition in a food mass packed at the end of a previously dug burrow. This pattern of digging the nest first and then provisioning it is maintained in groups II and III. In groups IV, V and VI the food ball is prepared first and then buried.

The most primitive form of nidification known, the closest thing to the food "sausage", is the nest of *Liatongus monstrosus* (Bates) an oniticelline whose members eat debris piles associated with nests of the leaf-cutter ant, *Atta mexicana* (Smith). The nest of *L. monstrosus* is a more or less vertical burrow with two or three branches which adults, especially the female, fill with unprocessed debris (Fig. 6). After the first 10 cm of debris are packed into the bottom of the burrow, the female lays an egg into a hollow, which is not a previously built chamber. Another 10 cm of debris is added and provided with an egg, and so on, until there are as many as 11 eggs between the two or three "sausages". There is no soil partition or anything similar between the debris portions containing each egg (Halffter, Anduaga and Halffter, 1976).

A larva eats the debris surrounding it. Once it reaches the end of its development, it builds a pupal cell by means of successive deposits of dung laid out around itself, touching the burrow walls in the form of concentric rings and capping it with concentric fecal rings (Edmonds and Halffter 1972). Larvae of *L. monstrosus*, the species with the least developed nidification behavior, have the best built pupal cells so far found among Scarabaeinae.

Preparation by a third instar larva of its own pupal cell, consisting entirely of larval feces, is a primitive feature found only in Group I (Edmonds and Halffter 1972). In other groups, a pupal cell is the brood-ball made by a female after her youngster has eaten the food stored inside. The outside walls, which are cemented by the excrement of the larva itself, remain standing.

The nest characteristic of *Dichotomius carolinus* (L.) (Coprini-Dichotomiina) is similar to that of *Liatongus monstrosus*. An initial mass of dung is packed by a female, fragment by fragment, in the final burrow that has been widened. The female deposits an egg in this mass. Before preparing a second mass nest, a female closes off the first one with a wall of dirt that separates each larval compartment until the end of development (Fig. 7). *D. carolinus* individuals nest at the expense of a manure pat and therefore quantity of available food is limited and not practically unlimited as for *L. monstrosus* individuals. Each nest consists of no more than two mass-nests, but each female prepares various nests in her lifetime.

Very frequently nests are occupied by both male and female of *D. carolinus* and *L. monstrosus*. Incipient cooperation exists in providing for the nest even though the greater part of the task is borne by a female, who digs the burrows with little participation by the male and who prepares the mass nest. However, a male does his share by taking food piece by piece to the female at the entrance of the nest or the upper part of the burrow which she packs. This incipient cooperation is characteristic of Group I; in more developed nidification patterns male participation is greater.

Within Group I handling of the food mass meant for the larva, its isolation, and protection of the egg are perfected. Females of *Onthophagus* (Onthophagini) and of various genera in Dichotomiina (Coprini) and Onitini, prepare a special chamber for an egg, in which it is placed in an upright position and cemented at its base by a substance secreted by the female. Also, in some species of *Onthophagus*, a female covers a burrow wall with a cementing substance before the food is packed. This substance forms a partially waterproof covering around food and egg.

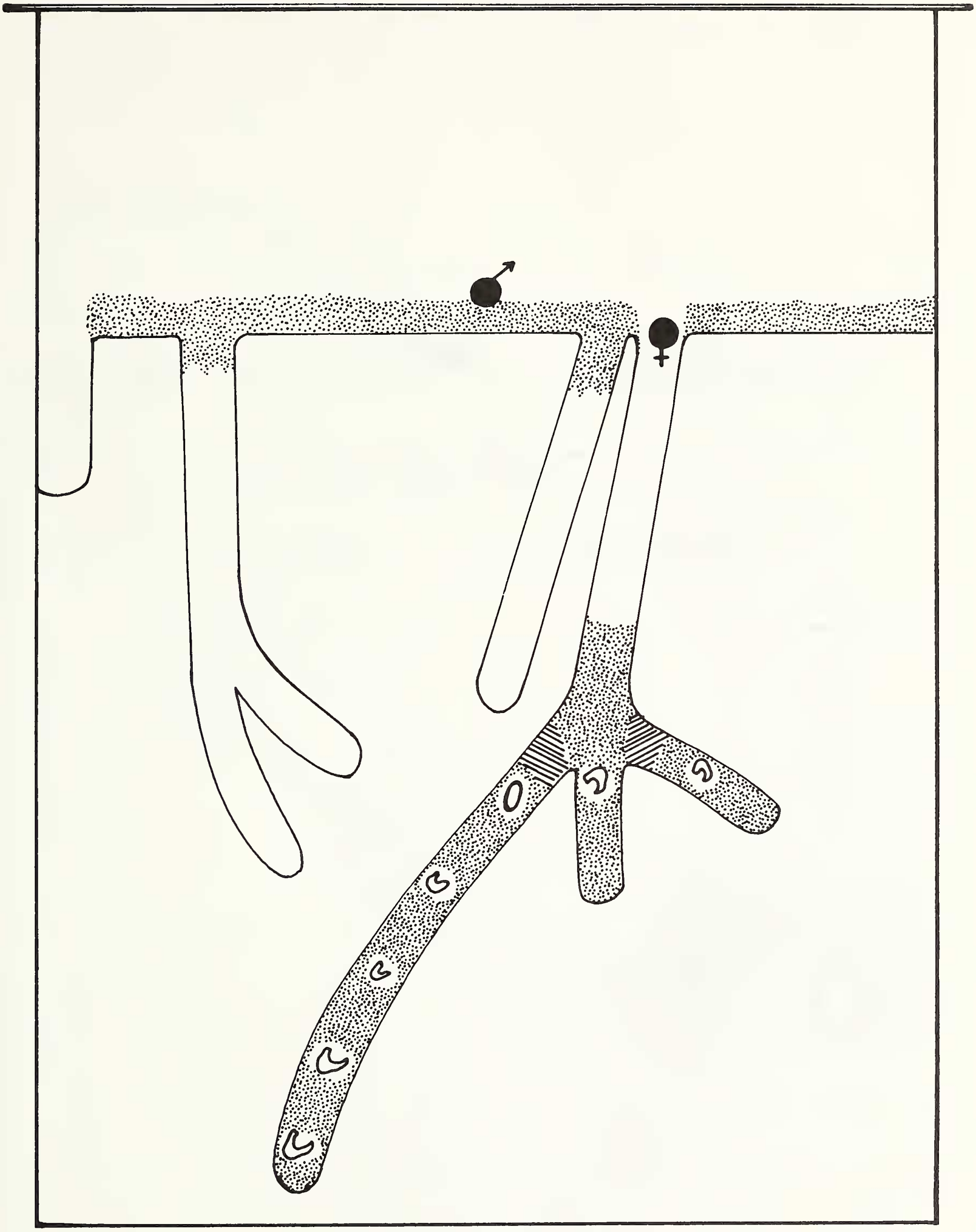


Fig. 6. Nest of *Liatongus monstrosus* (Bates). The dotted represents the debris; the positions of the male and the female are shown.

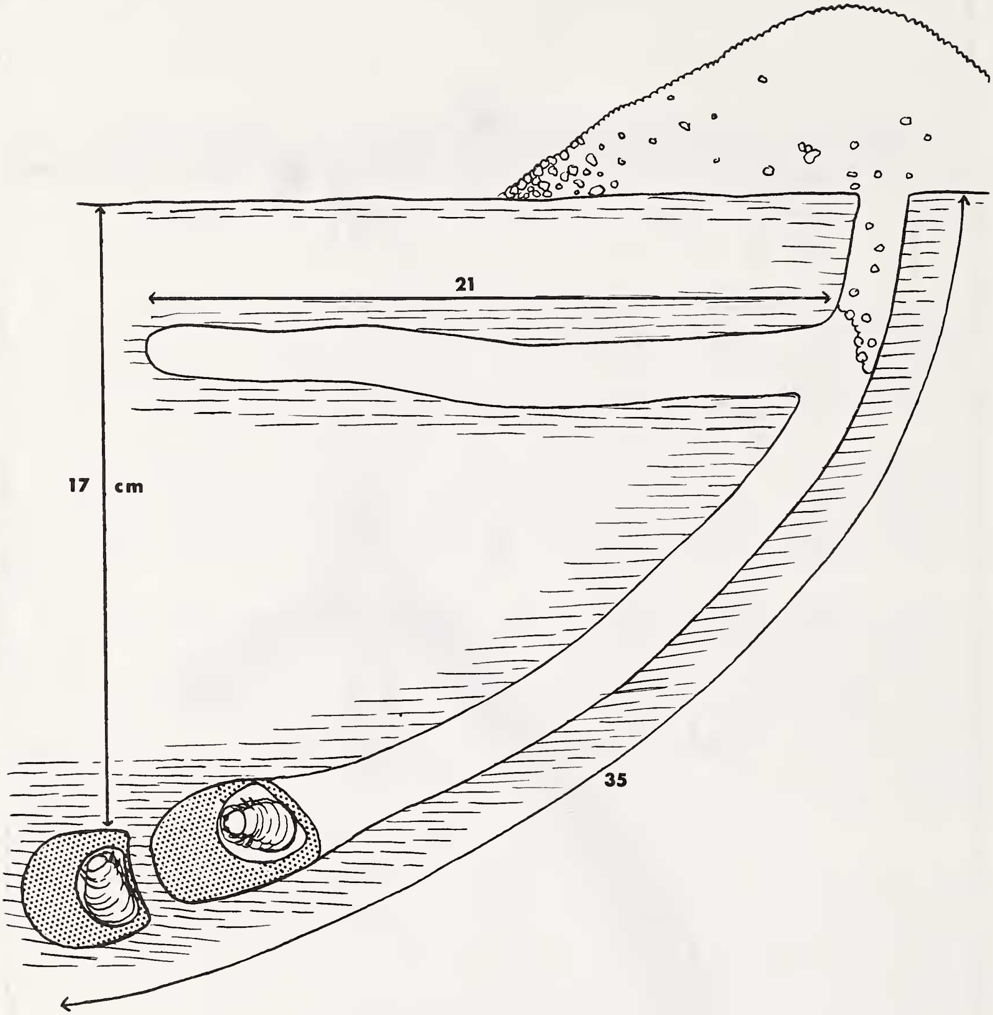


Fig. 7. Nest of *Dichotomius carolinus* (L.) (Halffter and Matthews 1966).

In Group I, an egg is deposited without prior preparation of a cell in the food mass (in the front or back of it). As we pointed out, within this same group is developed the preparation by a female of an egg cell before oviposition (for example in *Neocanthidium* and *Canthidium*). The same occurs in Group III, but it reaches its greatest perfection in Group II, in which an egg cell has a layer of clay that separates it from the food.

A parallel evolutionary process is present in the ball-roller forms. The egg cell is characteristic of group IV, as well as of *Eurysternus* (Group VI), but its greatest perfection – equivalent to that of Group II – is exhibited by *Canthon cyanellus* (Group V), in which it is placed on a knoll separated by a layer of earth from the food mass.

Isolation of an egg inside a chamber has undoubted value for survival, because it is thus protected against action by bacteria and fungi from the excrement or carrion accumulated by a mother for her youngster's food. Lack of a previously made chamber should be considered a very primitive feature.

The most complex nidification within Group I is that of *Neocanthidium* (Halffter and López, unpublished). Females of this dichotomiine make a truly elaborate brood-ball, and not simply a food-packed mass transformed into a nest by laying an egg. The brood-ball is pear-shaped, with the egg in the base of the upper cone; each ball (one to a nest) is isolated in a small chamber built in an enlargment of the nest-burrow. Only lack of an outer layer of dirt prevents inclusion of *Neocanthidium* nidification in Group II.

Fecundity is, with the possible exception of *L. monstrosus*, much higher in Group I than in groups II and III, which include more elaborate nidification procedures.

An example of ecological versatility in nidification has been published by Matthews (1972). It pertains to *Onthophagus parvus* Blanchard, one of the phoretic Australian species of the genus (formerly placed in *Macropocopris*) whose members live on kangaroos. Claws and apex of the tarsus are modified for clinging to hair; individuals congregate around the anal or cloacal openings: "During defecation, beetles converge on the emerging pellet and two or three get a grip on the pellet and drop with it to the ground . . . Once on the ground with the pellet, the beetles engage in a 'lively tussle' for possession of it, and one individual emerges as victor. This beetle may roll the pellet as much as a foot . . . pushing forward. The beetle then buried itself and the pellet . . . After 10 days the pellets were found to be unaltered externally but to be completely filled by a single larva, leaving only a fibrous outer wall 1mm thick".

In *O. parvus* there is a change in the usual nidification form of the genus since a female does not form the brood-ball fragment by fragment in a pre-constructed burrow; rather, it takes advantage of the natural ovoid which is the *complete* pellet, before desiccation renders it useless. Travelling on "the source", *O. parvus* adults take advantage of the pellets at the moment of defecation and thus avoid the tremendous expenditure of energy involved in search for small fragments of excrement scattered over large areas. This is only one of the adaptations of Australian Scarabaeinae in response to occurrence of dung pellets of marsupials and to coincidental lack of large droppings typical of placental herbivores.

Behavior in feeding and nidification of most scarabaeines (in the evolutionary line represented by the burrowers, as well as by ball rollers), corresponds to structure of feces of large herbivores: amorphous masses sufficiently large that upon hardening the outer surface preserves the plastic interior for several hours. Probably coprophagy of the group originated in this type of excrement.

Through specialization to certain ecological conditions (such as abundance of rodents in the arid regions of North America), some species became adapted to use of pellets of rodents, and even stenophagy develops. This same phenomenon is evident among those scarabs that use the feces of ovines and cervids.

Nevertheless, only in Australia, have adaptations to characteristics of pellets (those of marsupials) become profound, to the point that introduction of bovine feces (resulting from introduction of cattle) have not encountered a fauna of Scarabaeinae complex enough to exploit it or destroy it (although some Australian scarabs are attracted by bovine or by human excrement, most depend upon the excrement of marsupials).

Aside from the above-mentioned, adaptations to characteristics of pellets (dissemination of feces, rapid hardening, and desiccation) include burial of groups of pellets in soil sufficiently deep that ground moisture permits their disintegration, and abundance of Canthonina species whose members roll but do not manufacture dung balls; rather take advantage of pellets or already existing small masses of feces. (see Bornemissza 1971, Matthews 1974).

Group II

Group II nidification behavior is characterized by use of soil by a female. Such soil has a high percentage of clay and is used in construction of a protective layer around the food and the egg and a partition between egg and food.

From an evolutionary point of view, such behavior supposes appearance of a modelled complex whose end product is the brood-ball covered with clay (Fig. 8). The process involves careful formation by a female of a sphere of food at the end of a burrow. A layer of dirt from the burrow wall is then pressed around it. Packing of the soil reduces its volume giving rise to a layer of air around the brood ball. Thus, the end of the burrow becomes a chamber. The layer of air functions as a protective device in addition to that of the layer of soil. A female travels over the ovoid not only packing the dirt, but also modelling the surface. The process of food packing is similar to that carried out in Group I, leading me to assume that Group II behaviour has been derived from Group I. In *Dichotomius, D. carolinus* individuals have nests of the Group I type while *D. torulosus* (Eschscholtz) individuals manufacture brood-balls typical of Group II. With the exception of *Dichotomius*, nidification Group II is restricted to the Phanaeina, a subtribe of American Coprini.

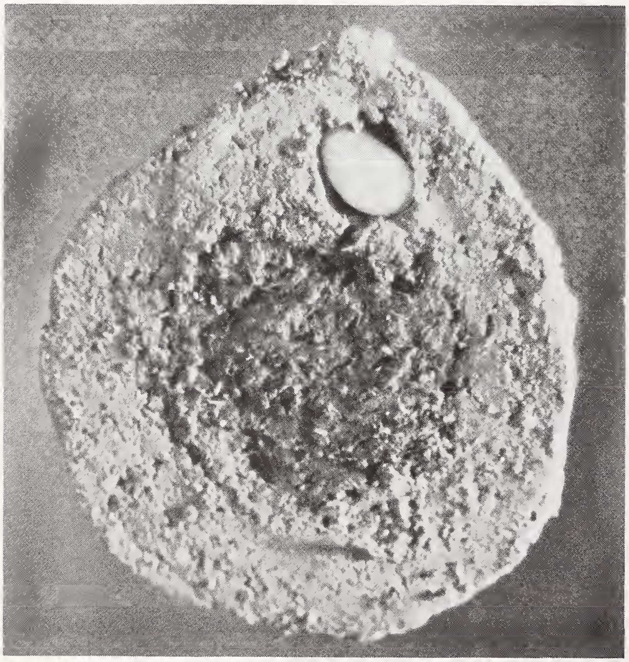


Fig. 8. Brood-ball of *Phanaeus daphnis* Harold.

A test of the efficiency of Group II nidification is the extremely low fecundity encountered in *Phanaeus*. A female, under natural conditions produces a maximum of 6 brood-balls in her life time. Under optimum laboratory conditions, the biotic potential is only 12 eggs (Halffter and López 1977).

In two Mexican species of *Phanaeus*, joint male-female provisioning of burrows during the period of gonad maturation prior to nidification has been studied by Halffter, Halffter and López 1974. Very elaborate cooperation between the sexes results in construction of a home: the burrow in which food is protected from competitors. Male-female cooperation in the reproductive behavior of *Phanaeus* suggests a principle of subsocial behavior (Fig. 9). Cooperation continues during nidification although formation of a bisexual couple does not depend on copulation. Copulation occurs on the surface at completion of oocyte maturation with a male that is rarely the original partner of the female during gonad maturation, (Halffter and López 1977). Copulation, which apparently occurs only once in the lifetime of the female, is an event of less importance in the complex bisexual behavior of *Phanaeus* centered around cooperative construction of burrows for food or nests.

In localities with high competition that results from many scarabaeines for each dung pad, adults of various species of *Phanaeus* (Halffter and Matthews 1966, Halffter, Halffter and López 1974), separate fragments of excrement and rolling them; an action undertaken principally by females alone.

This is convergence in behavior with the rolling by adults of Scarabaeini (Groups IV and V), and fulfills the same purpose: a small portion of food is removed from the area of intense competition, but the action is carried out in a very different manner. A *Phanaeus* adult does not undertake prior preparation of a brood-ball and the portion of excrement is made to roll, a beetle pushing it (up and forward) with its head and pronotum on the underside of the portion, that usually has an approximately spherical shape. Perfect and rapid rolling typical of Scarabaeini does not take place. On the other hand, these *Phaneus* adults retain the excavating habits typical of the Coprini.

This is not the only instance of evolutionary convergence between the two major lines of behavior as a response to similar ecological pressures. Other examples are protection of the brood-ball with an external layer of earth and separation of the egg chamber from the food mass by a small layer of earth, a typical behavior of Group II, that appears independently in at least one species of Group III (*Copris boucardi* Harold, personal observation), as well as in Groups IV to VI that make up the other major evolutionary line of behavior, reaching great perfection – comparable to that of the *Phanaeus* – in *Canthon cyanellus*; perfection of the egg chamber is also developed independently in the two great lines; and even phoretic association of adults with vertebrates, as a form for the rapid use of excrement that remains dispersed: *Onthophagus* in Australia, Dichotomiina and Canthonina in America (Halffter and Matthews 1966, Matthews 1972, observations of G. and V. Halffter on *Glaphyrocanthon subhyalinus* Harold associated to monkeys – *Alouatta* – in Palenque, Chiapas, Mexico, in order to use the excrement that remains in the upper parts of the rain forests).

Group III

Group III nidification behavior is characterized by multiple brood balls formed from an initial dung mass which are cared for by the parents. It is known only in Coprina and *Cephalodesmius*, although *Onitis* behavior is obviously an antecedent. In both genera, beetles initially remove a layer of soil around a recently buried mass of dung, but this soil is not pressed against the food to form a crust; rather it is firmly pressed against the burrow walls so that a large chamber is formed around the dung mass. Thus, there is only a layer of air around the food and no layer of soil as in Group II (Fig. 10). Adults of *Onitis* bury a large mass of dung

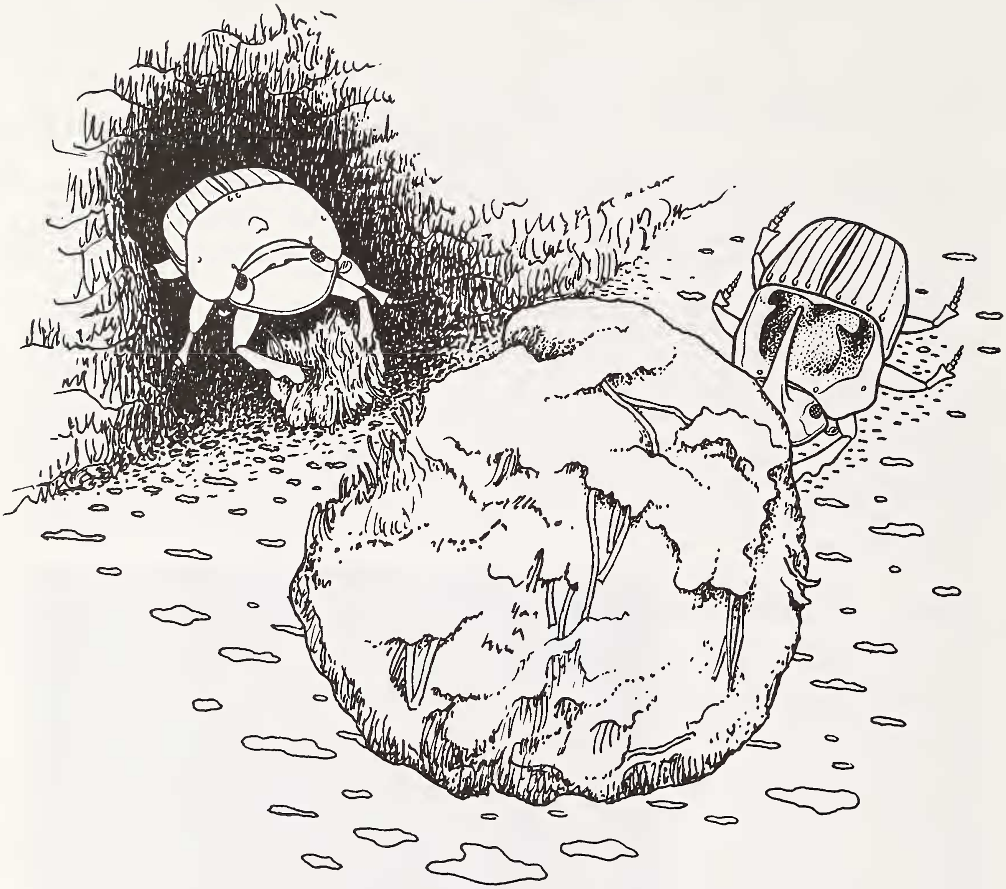


Fig. 9. *Phanaeus daphnis* Harold. Male-female cooperation. The male takes dung that the female has rolled to the entrance of the burrow; the female introduces it fragment by fragment (Halffter, Halffter and López 1974).

in which five eggs are placed without making independent ovoids. It is not known how long a female remains with the developing larvae. *Copris* adults follow the same preliminary stages but the female separates a portion of the large initial mass and molds it into an ovoid after the first egg has been laid in it. It cuts another portion after laying the second egg, and so on, until the original mass is divided into several separate brood balls, each one of which contains an egg. Halffter and Matthews (1966) presume that this method is an improvement over the *Onitis* method because each larva is assured of an adequate amount of food, thus eliminating interlarval competition.

It is not known exactly whether *Onitis* has brooding behavior during development, which has led me to exclude this genus from Group III. What I do know for sure is that *Onitis* behavior is a logical antecedent of coprine behavior (Group III).

The basic characteristic of Group III behavior is that the female remains with the brood-balls and cares for them until adult progeny has emerged. To judge by the low mortality recorded during development and the very low fecundity, I conclude that presence of the female substitutes for the clay layer characteristic of Group II behavior, thus affording protection to the brood.

Until now, Group III included only the subtribe Coprina (Coprini), a highly homogeneous taxon. New, unpublished data by the Australians G.B. Monteith and R.I. Storey lead me to incorporate *Cephalodesmius* (Scarabaeini-Canthonina), which is very distant taxonomically (for a summary of behavior of adults of this genus, see Matthews 1974).

Like Coprina, *Cephalodesmius*[1] adults form a multiple nest with male-female cooperation, with brood-balls tended by the female. This behavior is characteristic of some other Canthonina (Group V), but unlike them and like the Coprina from Group III, *Cephalodesmius* adults dig the nest beforehand. Moreover, a pair of *Cephalodesmius* adults occupies the nest during their entire adult life. Surface provisioning is mainly carried out by a male, or perhaps by him alone. A female makes a "cake" and after it has properly fermented, she manufactures and supplies from 6 to 10 brood-balls with eggs. The "cake" is of leaves, flowers and small fruits, and perhaps a fragment of dung which the male gathers from the surface, and, securing it with the hind legs, takes to the nest by walking backward. There, the female makes the "cake" by adding her own excrement and perhaps that of the male. This provisioning is exactly as in Groups I and II and in Coprina. In a period of two weeks, microbial activity transforms this compact mass into something very similar to animal dung, and with this substance the female makes brood-balls.

The relationship between adults and developing larvae is closer in *Cephalodesmius* than in other Scarabaeinae. Adults lick a liquid that seeps from the mass undergoing fermentation, even though some individuals also consume excrement that they might find on the surface. This provides for continuous food contact with the nest. However, there is also another behavioral feature not seen in any other Scarabaeinae: once the brood-balls have been completed and during larval development, a female places more leaves on the outside of each brood-ball. These leaves are brought by her mate and are mixed with flows of excrement from the larva and from the female. Addition of this new material increases size of the brood-ball. Larvae stridulate audibly in these brood-balls. Monteith and Storey believe that this may be a means of contact with the parents.

As the larvae approach pupation, the female closes off the chamber containing the brood-balls, and stays with them until progeny emerge. The male remains in the upper part of the burrow where he dies. The behavior of a *Cephalodesmius* family has all the features of a truly subsocial relationship between parents and offspring, with brooding behavior, food, and common homes.

---

[1] The process has been studied in detail in *C. armiger* Westwood; the same behavior is followed by the other two species of the genus *C. laticollis* Pascoe and *C. quadridens* MacLeay, in its basic features.

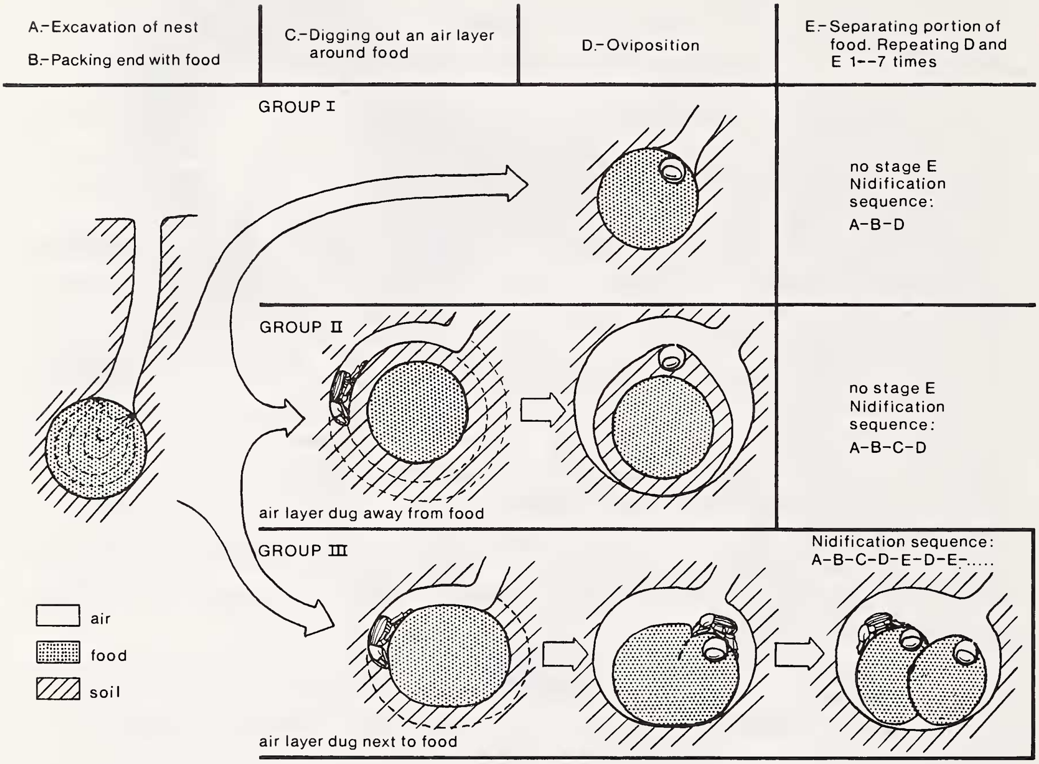


Fig. 10. Evolution of nidification from the food "sausage" in group I, II and III of nidification (Halffter and Matthews 1966).

Group IV

Most adults of the tribe Scarabaeini (the ball-rollers) exhibit a nidification behavior completely different from the three preceding nidification groups, and this pattern constitutes Group IV. The most consistent feature is that members of this tribe (except *Cephalodesmius*) do not pack food into a previously built burrow, provisioning it fragment by fragment. Moreover, even when a ball is not fashioned at the food source, the pellet or rolled fragment is buried just as it is by undermining it, and food and beetle gradually assume a position just below the surface. The developing young are not attended by the parents.

To understand evolution of such behavior, ability to make a ball from a large mass of food must be distinguished from capability of rolling a well-shaped ball or a pellet.

Matthews (1974) names 11 related genera of Australian canthonines, adults of which do not make a ball from a manure pat, even though they roll marsupial, sheep or rabbit pellets. He presumes that these genera remain in a primitive evolutionary stage prior to capability for ball-making. These data support the hypothesis by Halffter and Matthews (1966), according to which rolling of small pieces of excrement is a prerequisite to the ball-making process.

Undoubtedly, survival and relative abundance of these primitive Canthonina in Australia is directly related to an ecological factor: abundance of pellet-shaped excrement and lack of manure pats and large dung masses before arrival of man and livestock.

In Scarabaeini, the ball is made by a male who is then joined by a female during rolling, or is prepared jointly at the food source itself. If there is no sexual cooperation, as Wille (1973) described for *Megathoposoma candezei* (Harold), copulation takes place on the food source and the female prepares, rolls and buries the ball, which becomes a brood-ball without any cooperation by a male.

Positions of both sexes during rolling vary from genus to genus, even though males (with the possible exception of some of *Gymnopleurus*) are more active, whether pushing or pulling. Burial a few centimeters below the surface is also performed by a male, after which copulation takes place and his mate shapes the initial ball into a brood-ball where she oviposits. Adults of some species follow a pattern with a result similar to that of the Group II Coprini in which a female adds on an outer layer of clay to the brood-ball.

Group V

Group V nidification results in multiple nests prepared by ball-rollers (Scarabaeini). Each nest includes several balls which are brooded by the female, as is characteristic of Group III. However, the nest formation process is completely different.

Halffter and Matthews (1966) mention multiple nests of various species of South American *Canthon*: *C. bispinus* Germar, *C. muticus* Harold, *C. edentulus* Harold and *C. virens* (Mannerheim). Not having precise observations about the way in which nests had been made, nor about possible brooding behavior, they considered these nests to be within "Aberrant Nidification Behavior" (that is, those not accomodated by one of the four groups proposed by them) while pointing out: "The very unexpected brooding behavior ascribed by Judulien (1899) to two of the same three species of *Canthon* in Argentina (*bispinus* and *edentulus*) and to *Malagoniella bicolor* (Guerin) and *M. puncticollis tubericeps* (Gillet), requires confirmation. If confirmed, this behavior represents the independent acquisition by some Scarabaeini of the brooding behavior known elsewhere only in the Coprina (Croprini)". Beside the above mentioned examples, an Australian canthonine with multiple-nesting is known: *Aulacopris maximus* Matthews 1974; Waite 1898).

All of these should remain in Group V which has been established on the basis of behavior of adults of an American canthonine, *Canthon cyanellus cyanellus* LeConte, studied for several years (G. Halffter and V. Halffter, unpublished).

In Group V, each ball is formed at a food mass, rolled to the nest and transformed into a brood-ball at that point. This is typical of Scarabaeini members adapted to formation of a multiple nest.

In *C. cyanellus* the pair becomes associated at the food source (carrion or small animals undergoing decomposition). Copulation takes place there and may be repeated at the nest site. Male and female collaborate in cutting fragments with which they form the ball, which is rolled jointly. During rolling, a layer of soil is added, which is increased in size by the female by adding soil with the fore legs at the site where the multiple nest will be established.

At the upper part the female adds a mound of soil which modifies the originally spherical shape. She oviposits in this mound.

A brood-ball prepared in this manner is left by the parents who go on to form a new ball, which they roll to the site where the previous brood-ball is located. Successive balls are rolled and transformed into brood-balls at the rate of one per day. The nest has from 2 to 6 balls, 3 average (Fig. 11). Unlike the Group III pattern, a female prepares several nests during her adult life but does not make a new nest until the adults emerge.

During larval and pupal development until the emergence of the new generation, a female remains in the nest tending the brood-balls, preventing mold development on the outer surface. The associated male also remains in the nest, even though not in a compulsory and constant manner as the female.

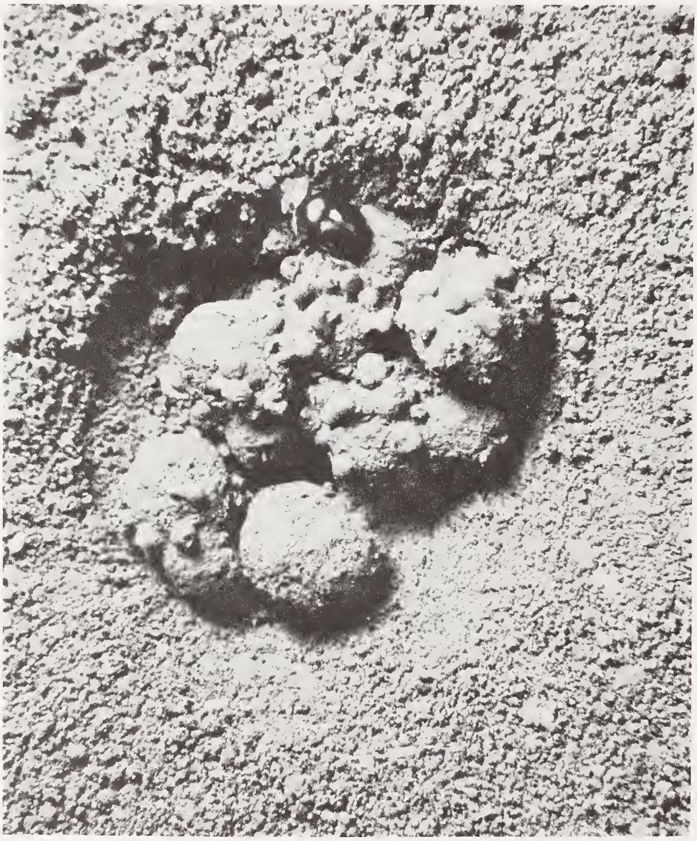


Fig. 11. *Canthon c. cyanellus* LeConte. Multiple nest. The brood-balls are located in a lightly dug crater in which the male and the female are found.

Group VI

Includes only the Neotropical genus *Eurysternus* (Eurysternina, Scarabaeini). Nidification of *Eurysternus* is strange and difficult to place within the presumed evolutionary sequence of nesting habits of Scarabaeinae, just as it is difficult to place this genus taxonomically. The following account is based on unpublished results of recent work by G. Halffter, V. Halffter, P. Reyes-Castillo and Yrma López.

Eurysternus adults make balls but are incapable of rolling them even though they can push them clumsily with head and pronotum. They have multiple nests and both parents brood; the female makes several nests. An extraordinary feature of their behavior is that a large number of feeding balls and brood-balls are made, of which many are abandoned or destroyed.

In the species we have studied in detail in the laboratory (*E. magnus* Laporte, *E. balachowskyi* Halffter and Halffter and *E. mexicanus* Harold) some adults ate directly from the manure pat, without making balls, for periods up to 200 days. Nidification comprises three successive stages: 1) nuptial feast, 2) experimental nidification, 3) final nidification (Fig. 13-14). Adults of *E. magnus* merge stages 2 and 3.

The large nuptial feast begins suddenly with formation of many balls (up to 17 per female for *E. magnus*, 55 for *E. balachowskyi*, 14 for *E. mexicanus*).

Only females of *E. balachowskyi* make balls. This is probably true of *E. magnus*, too. The balls remain close to the dung pat, in a more or less finished state. As of this moment the pair is formed and will not separate during the remainder of the nidification process. Some of the balls are eaten a few hours or days later, others are retouched and moved from place to place by the male or female parent. Many of the balls are partially devoured and then abandoned; some are abandoned untouched.

In *E. magnus*, from this disorderly feast final nidification takes place, 15 to 28 days after beginning of ball formation. Nidification begins with the very shallow burial of three of the balls, which are first undermined to form a crater into which a few more balls are pushed and which remain at the surface.

Initial oviposition takes place immediately before undermining the crater or during the first few hours of digging. Inside a crater, a female continuously retouches the balls, sometimes assisted by her mate. Males very frequently and females infrequently eat some of the dung pat. Some of the balls in the crater are partially eaten or used to remodel others. At the end of a 7-day period there are three brood-balls which the female covers with soil and broods (with the occasional company of the male) until hatching occurs. Once the process, which lasts several days, is finished, the female starts a new nest with another nuptial feast. We do not know if under field conditions, the same male accompanies her.

Eurysternus balachowskyi adults perform a nuptial feast exactly as described above. The female makes the balls frantically for from 2 to 3 months. Most of them are abandoned or partially consumed. Next, as in *E. magnus*, a crater is dug beneath some balls and others are pushed into it; three balls are provided with eggs and are partially covered with soil. Parental brooding occurs, especially by the female, but with a difference from other species: at a certain moment, female or male attacks a part of the balls containing eggs, while both continue to care for the others. A few days later, the female or male destroys the remaining brood-balls and they both abandon the nest. Some brood-balls may survive this ovicidal frenzy and complete their development, but it is a random process.

After a direct feeding period in dung the above activities are repeated, perhaps several times, with resulting abandonment of the craters with partially consumed balls. Final nidification (stage 3) represents efficient brooding by the female. She chooses two brood-balls and places them on the surface so that they touch each other. She then digs a furrow around them and covers them with soil. The furrow is made deeper and wider until the balls are elevated with a minimum of support. For forty days the female cares for this nest without attempting to destroy it. Following hatching of eggs and after a month of feeding directly in the dung, the female begins once again manufacture of balls.

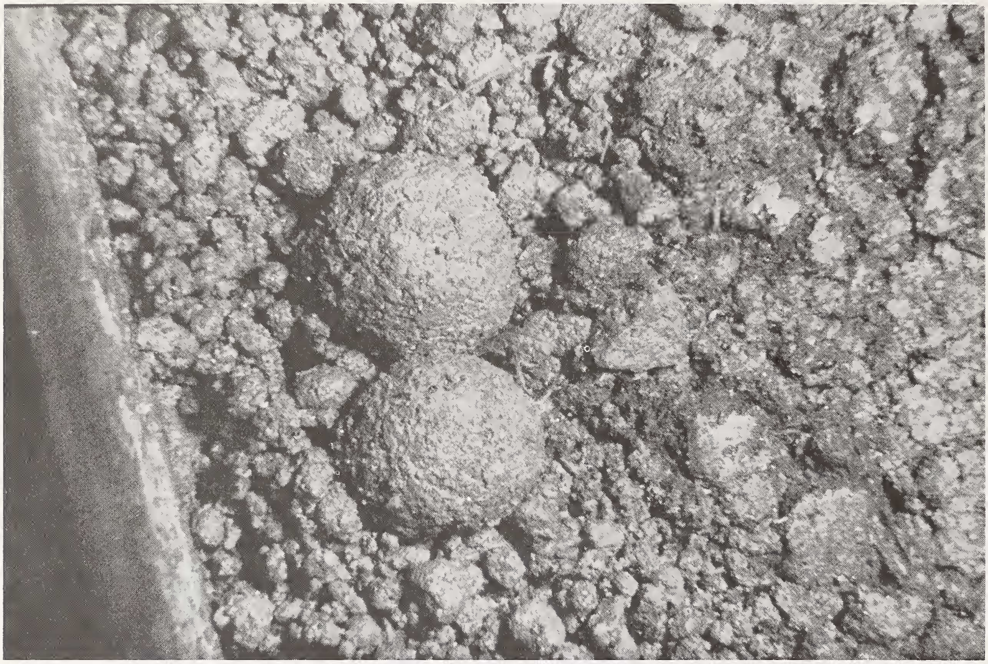


Fig. 12. *Eurysternus balachowskyi* Halffter and Halffter. Initial stage in the preparation of final nidification.

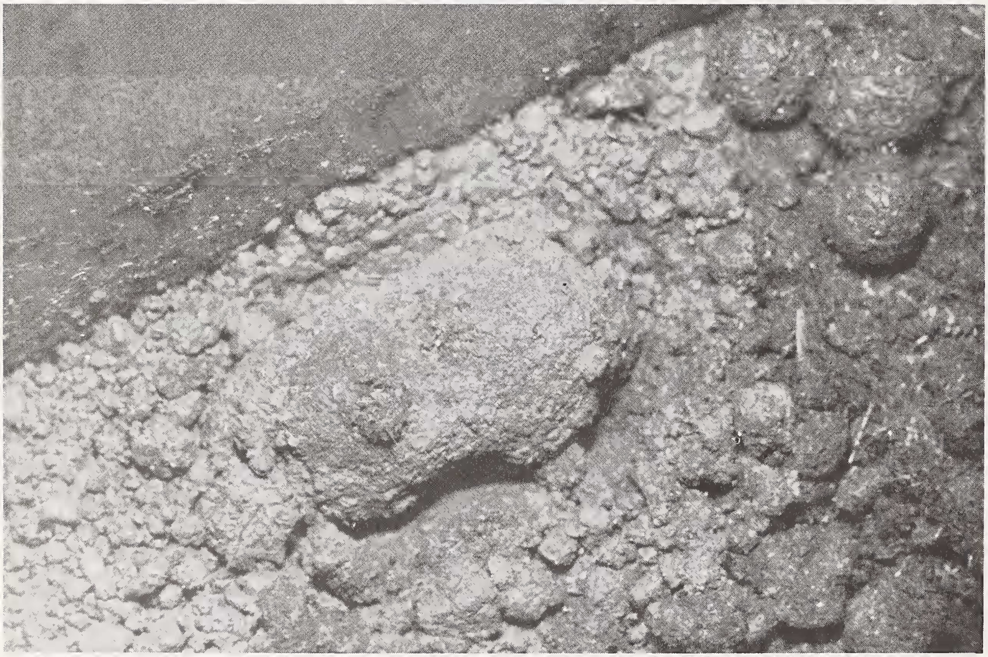


Fig. 13. *Eurysternus balachowskyi* Halffter and Halffter. Final nest surrounded by a protector furrow; at the top, abandoned balls.

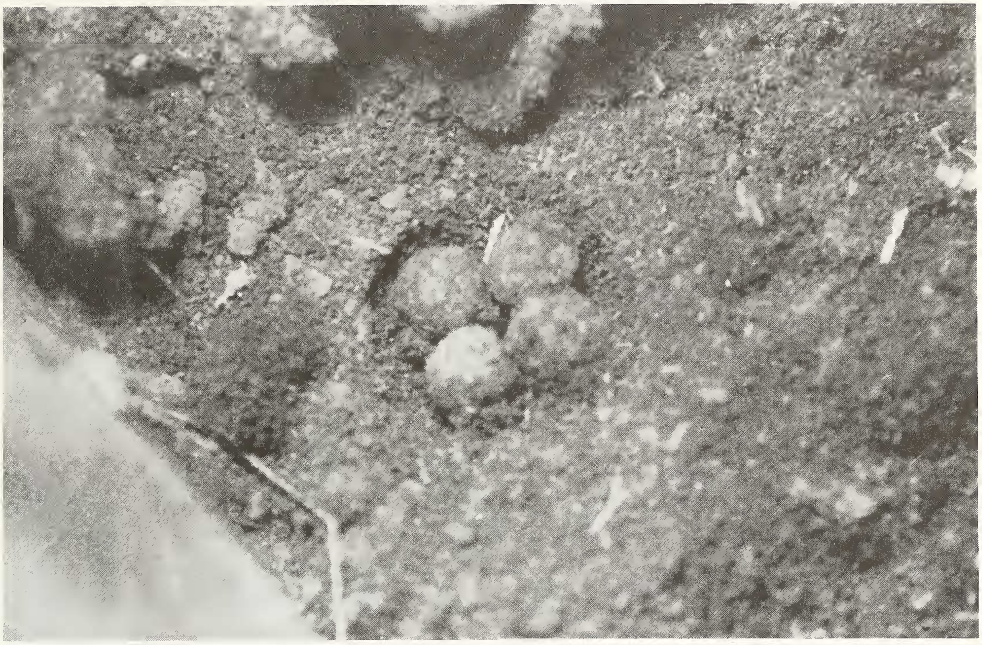


Fig. 14. *Eurysternus mexicanus* Harold. Final nest.

Adults of the third species, *E. mexicanus*, have a very large nuptial feast. A crater is formed, and brood-balls (generally 3) are cared for. Copulation takes place several times and the balls in the crater are destroyed, including the brood-balls, by male and female (sometimes one ball is spared and the egg contained therein hatches). The process is repeated four times in a period of four months. The final nest is a dug-out hollow between manure pat and soil, each containing 3 to 9 brood-balls each receiving minimal attention from the female, even though neither of the parents harm it.

Characteristics of Group VI are: a) construction of numerous balls at the beginning of the nidification process (preferably or exclusively by the female); b) consumption or abandonment of these balls; c) no ball rolling; d) multiple nesting of one or two different types in the same species; e) very well developed brooding mainly by the female, but also with the participation of the male; f) a stable male-female bond defended from outsiders when nidification is in progress; g) destruction of some or all of the brood-balls after a period of care; h) construction of several multiple nests by the female with intermediate periods of direct feeding in excrement without manufacturing balls.

Nidification of *Oniticellus cinctus* F. (Oniticellini) may be similar to that of *Eurysternus*, with numerous brood-balls in chambers made inside horse manure (Gardner 1929, Bornemissza 1969). I place it in Group VI provisionally, until more information is available about its behavior.

DISCUSSION

A preliminary analysis of the nidification groups leads to three conclusions which support each other in spite of their apparent contradictions:

1. - Distinguishing features of the tribes and subtribes of Scarabaeinae include nidification

behavior.

2. - The clear-cut, static nature of taxonomic groupings differs from the dynamic nature of the evolutionary process, such that there is intratribal variation in details of the nidification process. Thus, of the 6 tribes that make up the subfamily, three of them, several of the subtribes and a genus do not conform to a single nidification group, but to two groups, ranging from very primitive stages to highly developed forms.
3. - A solution to the problem of excrement handling is at the root of each one of the evolutionary trends in nidification. In other words, in the less developed stages, the *nest is a derivative of the burrow or food ball*. Once the time comes for reproduction, a beetle uses modifications of feeding behavior for mechanisms established by adults to protect the food supply. In the more developed groups, relationship between food behavior and nidification may be less clear and only obvious in relation to what takes place in the most primitive group of the lineage.

SUMMARY

In summary, ecological pressures that affect excrement and its spatial distribution determine food behavior patterns. The latter, in turn, affect basic nidification types, which affect the possibilities of cooperation between sexes. Bisexual cooperation becomes a determining factor in evolution of nidification types and appearance of brooding behavior. Bisexual behavior, as well as relations with the young, lead to appearance of an incipient subsocial life in the most advanced types of dung beetle nesting. Such subsocial behavior may become independent of the reproductive process and may develop into a male-female cooperation to prepare, provision and protect a home from the environment as well as to defend it from competitors.

ACKNOWLEDGEMENTS

I extend special thanks to G.B. Monteith and R.I. Storey, the University of Queensland, Australia, for their unpublished observations on *Cephalodesmius*. Eric G. Matthews, the South Australian Museum, Adelaide, contributed observations and comments. For several years I have received the enthusiastic collaboration of Violeta Halffter (*Liatongus monstrosus, Canthon cyanellus, Eurysternus* and revision of the bibliography), Yrma López G. (*Neocanthidium, Eurysternus*), Pedro Reyes-Castillo (*Eurysternus* and a broad field work), Sofia Anduaga (*Liatongus monstrosus*), Carmen Huerta and Sabina Gómez M. (*Canthon cyanellus*). W.D. Edmonds, from the California State Polytechnic University, during his stay at the Instituto de Ecologia, reviewed and corrected the translation from Spanish into English. His comments and observations were of great value to me. To all of these persons, I express my gratitude.

This work was presented at the XV International Congress of Entomology, celebrated in Washington in August, 1976. It was read by Howard E. Hinton, to whom I am very grateful.

REFERENCES

Bornemissza, G.F. 1969. A new type of brood care observed in the dung beetle *Oniticellus cinctus* (Scarabaeidae). Pedobiologia 9: 223-225.

Bornemissza, G.F. 1971. A new variant of the paracopric nesting type in the Australian dung beetle, *Onthophagus compositus*. Pedobiologia 11: 1-10.

Edmonds, W.D. and G. Halffter. 1972. A taxonomical and biological study of the immature stages of some New World Scarabaeinae (Coleoptera: Scarabaeidae).

Gardner, J.C.M. 1919. Immature stages of Indian Coleoptera. 6. Indian Forest Records 14 (4): 27-30.

Halffter, G. and E.G. Matthews. 1966. The Natural History of Dung Beetles of the Subfamily Scarabaeinae (Coleoptera, Scarabaeidae). Folia Entomologica Mexicana 12-14: 312 pages.

Halffter, G., V. Halffter and Y. López G. 1974. *Phanaeus* Behavior: food transportation and bisexual cooperation. Environmental Entomology 3(2): 341-345.

Halffter, G. and Y. López G. 1977. Development of the Ovary and Mating Behavior in *Phanaeus*. Annals of the Entomological Society of America 70 (2): 203-213.

Halffter, V.,S. Anduaga and G. Halffter. 1976. Etograma de *Liatongus monstrosus* (Bates) (Coleoptera, Scarabaeidae). Folia Entomologica Mexicana 36: 48-49.

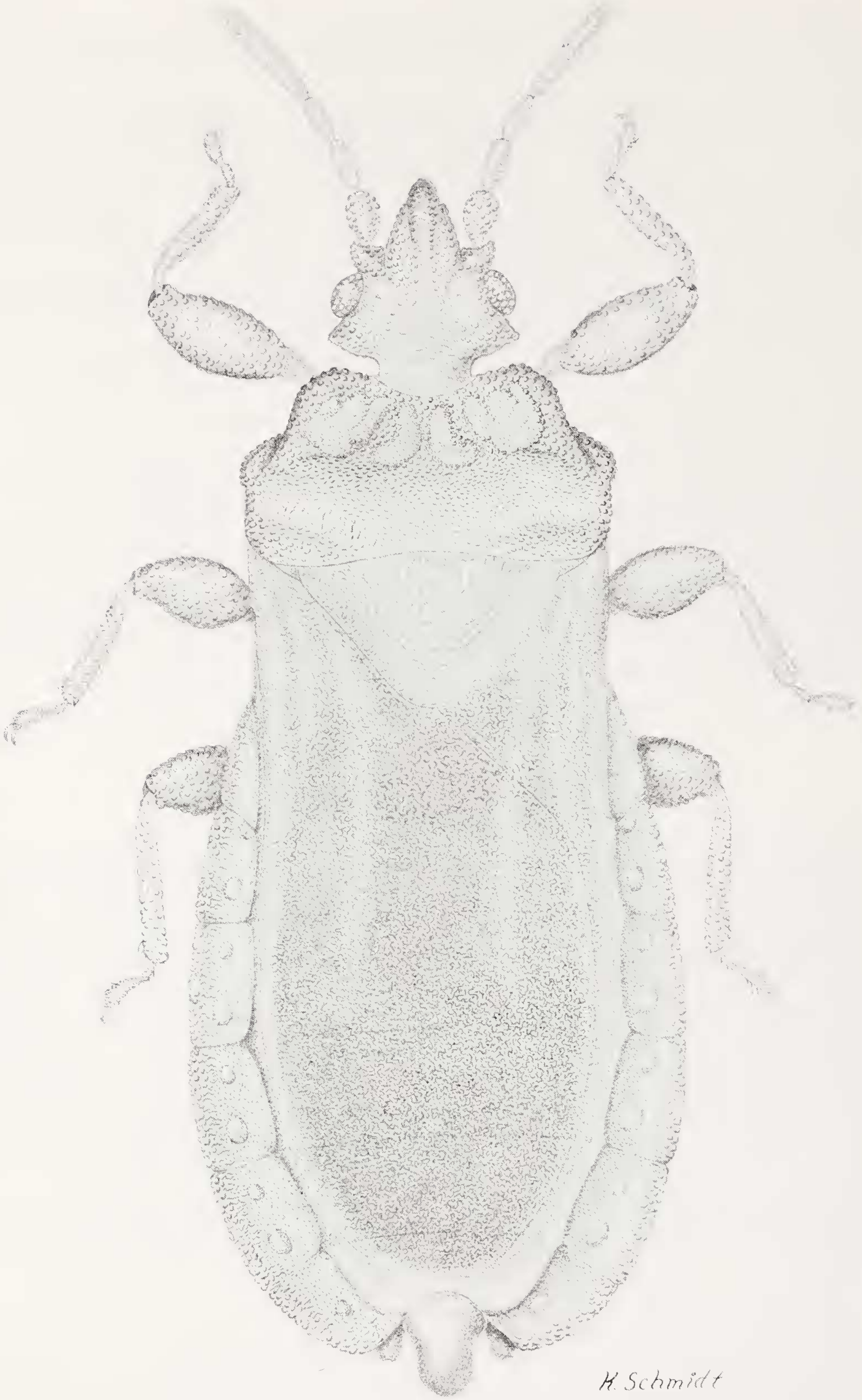
Judulien, F. 1899. Quelques notes sur plusieurs coprophages de Buenos Aires. Revista del Museo de La Plata 9: 371-380.

Matthews, E.G. 1972. A Revision of the Scarabaeine Dung Beetles of Australia I. Tribe Onthophagini. Australian Journal of Zoology Supplementary Series 9: 3-330.

Matthews, E.G. 1974. A Revision of the Scarabaeine Dung Beetles of Australia II. Tribe Scarabaeini. Australian Journal of Zoology Supplementary Series 24: 1-211.

Waite, E.R. 1898. Notes and exhibits. Proceedings of the Linnean Society of New South Wales 33, 803.

Wille, A. 1973. Observations on the behavior of a tropical rain forest dung beetle, *Megathoposoma candezei* (Harold). (Coleoptera: Scarabaeidae). Revista de Biologia Tropical 21(1): 41-57.



Frontispiece. *Aneurus patriciae* new species